Title	Inverse Bifurcation Problem in Mathematical Ecology and Related Wiener-Hopf Equations (Qualitative theory of functional equations and its application to mathematical science)
Author(s)	Iwasaki, Katsunori; Kamimura, Yutaka
Citation	数理解析研究所講究録 (2001), 1216: 115-127
Issue Date	2001-06
URL	http://hdl.handle.net/2433/41210
Right	
Type	Departmental Bulletin Paper
Textversion	publisher

数理解析研究所講究録 1216 巻 2001 年 115-127

Inverse Bifurcation Problem in Mathematical Ecology and Related Wiener-Hopf Equations

Katsunori Iwasaki* and Yutaka Kamimura†

*Faculty of Mathematics, Kyushu University
6-10-1 Hakozaki, Higashi-ku, Fukuoka 812-8581 Japan
iwasaki@math.kyushu-u.ac.jp (岩崎克則)

†Department of Ocean Sciences, Tokyo University of Fisheries
4-5-7 Konan, Minato-ku, Tokyo 108-8477 Japan
kamimura@tokyo-u-fish.ac.jp (上村 豊)

Abstract

This paper is a concise introduction to a recent work [6] by the authors on an inverse bifurcation problem in mathematical ecology. It deals with the identification of the nonlinear kinetics in a diffusional model of population dynamics from its bifurcation curve that describes the relation between growth rates and central densities of steady-state population distributions. It is emphasized that a certain class of Wiener-Hopf integral equations plays a principal role in our mathematical analysis of the inverse problem.

Key words: population dynamics, reaction-diffusion equation, nonlinear Sturm-Liouville equation, inverse bifurcation problem, nonlinear reaction kinetics, spatial heterogeneity, Wiener-Hopf equation.

2000 Mathematics Subject Classification: 92D40, 34C23, 47B35

1 Introduction

The history of mathematical ecology is, by and large, that of model buildings, starting from the Malthusian exponential growth model, through the famous Verhulst-Pearl-Reed logistic, up to more recent, innumerable, particular models, including the Ludwig-Aronson-Weinberger budworm equation,

for instance. (A brief review of them will be given in §2.) Those models have proved their utility during the course of extensive studies by many authors. Strictly speaking, however, it is not obviously clear why such a particular nonlinear kinetics was postulated, although it has certainly served as a very satisfactory working hypothesis in various situations. In fact, G.M. Murray, Jr. [12, p.19] points out that the logistic equations have been criticized frequently. See the references cited therein for more information.

In view of these, the nonlinear kinetics could be thought of as an unknown factor to be identified or reconstructed from observed data. In this sense, model buildings could be discussed from the standpoint of inverse problem. To the authors' knowledge, however, such an approach has hitherto attracted scant attention, even for one-species population dynamics. In a recent paper [6] the authors developed a mathematical analysis for approaching this sort of problem, and the aim of this expository article is to give a concise introduction to their results. As a beginning work, the paper [6] only deals with one-species, diffusional models of a particular class. More general and interesting multi-species models, involving complicated interspecific interactions, should be discussed in the future.

2 Single-Species Populations

To start from scratch, we begin by reviewing some classical, one-species models that do not take spatial patterns into account. One of the most classical models is the Malthusian exponential growth population (1780):

$$\frac{dv}{dt} = \lambda v \quad \rightsquigarrow \quad v(t) = v_0\, e^{\lambda t},$$

where $v = v(t)$ is the size of the population at time t and λ is the growth rate of each individual, v_0 being the initial population size at $t = 0$. This model is valid in an idealistic environment where an organism reproduces or dies with a constant provability, independent of the size of the population.

In a restricted environment the population is eventually limited by a shortage of resources and often shows a sigmoid growth. The logistic equation, originally proposed by Verhulst (1838) and then rediscovered by Pearl and Reed (1920), is a representative model describing such a sigmoid growth:

$$\frac{dv}{dt} = (\lambda - \beta v)v \quad \rightsquigarrow \quad v(t) = \frac{\lambda C e^{\lambda t}}{1 + \beta C e^{\lambda t}},$$

where λ is the intrinsic growth rate, β denotes the strength of the density dependence on the population size and $C = v_0/(\lambda - \beta v_0)$ (see Figure 1).

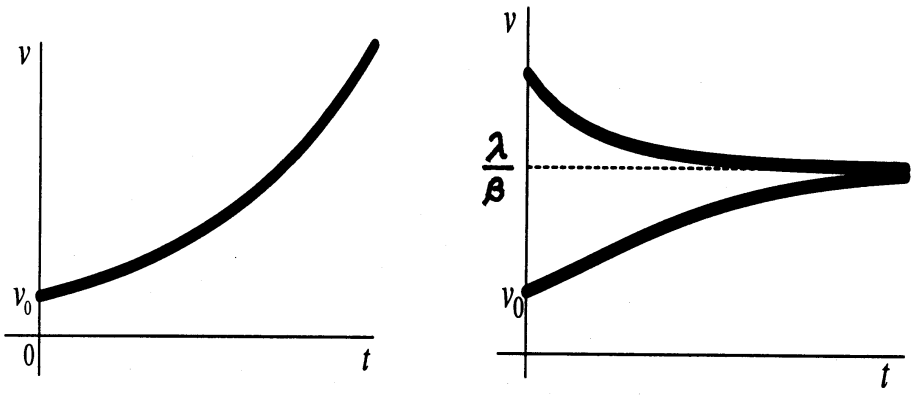

Figure 1: Malthusian population (left) and logistic population (right)

A more recent, particular model is, for instance, the spruce budworm equation due to Ludwig, Aronson and Weinberger [10] describing the population of a defoliating insect in the forest of New Brunswick:

$$\frac{dv}{dt} = v - \frac{v^2}{Q} - \frac{1}{R}\frac{v^2}{1+v^2},$$

where R represents the density of foliage. There is a large number of equations modeling the population growths of various species in various environments; too large to be quoted here or anywhere else.

3 Populations with Dispersal

The models in §2 do not take spatial patterns into account. However, the ecological situations can be understood only when populations of organisms are considered in both time and space. With the work of Skellam [17] (1951), the theory of random dispersal of biological population came into existence. His point of view naturally leads to discussing reaction-diffusion equations.

We present a few models with dispersal. The Malthusian population with dispersal is modeled by a linear partial differential equation:

$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial x^2} + \lambda v,$$

where D is the diffusivity, λ the intrinsic growth rate, and $v = v(x,t)$ denotes the spatio-temporal distribution of the population. Next, the diffusing logistic population is given by a nonlinear partial differential equation:

$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial x^2} + \lambda v - \beta v^2$$

Generalizing these two, one may consider the following equation:

$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial x^2} + \lambda v - g(v),$$

where $g(v)$ is a nonlinear reaction kinetics. This equation is sometimes called the KISS model after Kierstead and Slobodkin [7] and Skellam [17], provided that the boundary of habitat is completely lethal to species (the Dirichlet boundary condition).

4 Critical Patch Size and Steady-States

Steady-states often play an important part in population dynamics. To exhibit their role, we review the critical patch size problem for the KISS model:

$$(1) \qquad \begin{cases} v_t = D\, v_{xx} + \lambda v - g(v), & x \in (-L, L), \\ v = 0. & x = \pm L. \end{cases}$$

The *critical patch size* L_c is such a length that if $L < L_c$, the population distribution $v(x,t)$ vanishes as $t \to \infty$ (extinction); while if $L > L_c$, the population survives as $t \to \infty$ (outbreak, steady-state, periodic in time, etc.)

For the Malthusian population with dispersal, elementary Fourier analysis (Kierstead and Slobodkin [7]) shows that the critical patch size is given by

$$(2) \qquad L_c = \frac{\pi}{2}\sqrt{\frac{D}{\lambda}},$$

and an outbreak $\lim_{t\to\infty} v(x,t) = \infty$ occurs for $L > L_c$. For the diffusing logistic population, comparison arguments for nonlinear heat equations (Ludwig, Aronson and Weinberger [10]) show that the critical patch size is still given by (2) and a steady-state $\lim_{t\to\infty} v(x,t) = w(x)$ is achieved for $L > L_c$, where $w(x)$ is a nontrivial steady-state solution of (1). The latter example exhibits the importance of steady-states solutions.

5 Heterogeneous Environments

Generalizing the KISS model (1), one may think of a reaction-diffusion model in a *spatially heterogeneous* environment:

$$(3) \qquad \begin{cases} v_t = D\, v_{xx} + [\lambda - q(x)]v - g(v), & x \in (-L, L), \\ v = 0, & x = \pm L. \end{cases}$$

This model has a spatially varying growth rate $\lambda - q(x)$, where λ is a reference rate and $q(x)$ stands for a deviation from the reference at the location x, caused by the heterogeneity of an environment. It reduces to the KISS model when the environment is homogeneous: $q(x) \equiv 0$.

We turn our attention to steady-state solutions of (3). Note that only positive solutions are biologically relevant, since they should represent population distributions. They satisfy the nonlinear Sturm-Liouville equation:

$$(4) \qquad \begin{cases} D v'' + [\lambda - q(x)]v = g(v), & x \in (-L, L), \\ v = 0, & x = \pm L, \end{cases}$$

Assume the spatial symmetry: $q(x) = q(-x)$. Then positive solution $v = v(x)$ is also symmetric (in a certain reasonable situation): $v(x) = v(-x)$. It turns out that the *central density* $h = v(0)$ contains a dominant information about the population distribution, thus playing a principal role in our later discussions (see Figure 2).

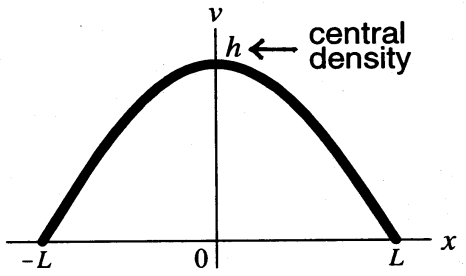

Figure 2: Population distribution

6 Bifurcation Curve

The relation between growth rates λ and central densities h of steady-states is described in terms of the *bifurcation curve* (see Figure 3):

$$\Gamma = \{ (h, \lambda) \in \mathbb{R}_+ \times \mathbb{R} : (\spadesuit) \},$$

where $(\spadesuit)$ is the condition that, under growth rate λ, there exists a positive solution $v(x)$ of (4) with central density $h = v(0)$. Note that the bifurcation curve $\Gamma = \Gamma(g)$ is determined by the kinetics g. For small kinetics g, the curve Γ becomes the graph of a function in h, and hence can be written

$$\Gamma : \quad \lambda = \lambda(h) = \lambda_1 + \mu(h) \quad \text{with} \quad \mu(0) = 0,$$

where λ_1 is the first eigenvalue of the linearized Sturm-Liouville equation:

$$(5) \qquad \begin{cases} D v'' + [\lambda - q(x)]v = 0, & x \in (-L, L), \\ v = 0, & x = \pm L, \end{cases}$$

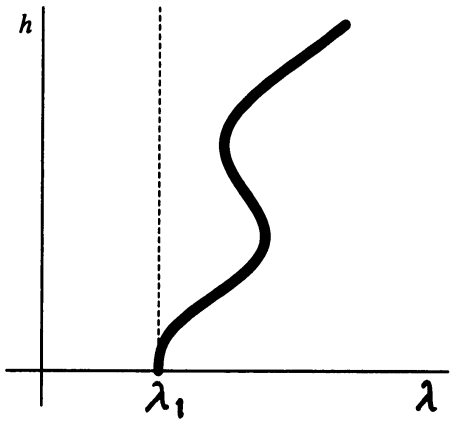

Figure 3: Bifurcation curve Γ

Now we can define the *direct bifurcation map* by associating to each nonlinear reaction kinetics g its bifurcation curve μ:

$$(6) \qquad \pi \ : \ g \text{ (reaction kinetics)} \ \mapsto \ \mu \text{ (bifurcation curve)}.$$

7 Inverse Bifurcation Problem

The inverse bifurcation problem addresses to consider the *inverse* of the direct bifurcation map π in (6); it contains the following three issues.

(i) **Existence**: Given a function μ, does there exist a nonlinear reaction kinetics g realizing μ as its bifurcation curve ?

$$\pi^{-1}(\mu) \neq \emptyset \quad ?$$

(ii) **Degree of freedom**: When the answer to question (i) is in the affirmative, how many such kinetics g exist ?

$$\text{Determine } \ N = \dim \pi^{-1}(\mu).$$

The dimension N of the iso-bifurcation manifold $\pi^{-1}(\mu)$ is referred to as the *degree of freedom* for feasible kinetics; (it *a priori* depends on μ).

(iii) **Effect of environment**: How the spatial heterogeneity $q = q(x)$ of an environment has influence upon the solutions to the two questions above, especially upon the degree of freedom N ?

$$N = N(q): \text{ how depends on } q \text{ ?}$$

8 Main Results

Main results of the mathematical analysis in Iwasaki and Kamimura [6] are roughly summarized in the following manner; see §3 of [6] for the precise statements based on a mathematically rigorous formulation.

Theorem 8.1

(i) *For any sufficiently small function μ, there exists a finite-dimensional manifold $\mathcal{M}_\mu$ that parameterizes all the small kinetics g having μ as their bifurcation curve.*

(ii) $\dim \mathcal{M}_\mu$ *is even and depends only on the heterogeneity of the environment q.*

(iii) *Conversely, for any nonnegative even integer N, there actually exist environments q such that* $\dim \mathcal{M}_\mu = N$.

In the terminology of §7, assertions (ii) and (iii) mention that the degree of freedom $N = N(q)$ is a nonnegative even integer, depending only on the spatial heterogeneity q of the environment, namely, independent of the bifurcation curve μ, and that any nonnegative integer N can be realized as the degree of freedom $N(q)$ for some environment q.

We remark that $N = 0$ for the KISS models $q(x) \equiv 0$.

9 Degree of Freedom

It is interesting to explore the properties of the degree of freedom $N(q)$. The following two are results in this direction.

(i) If $\tilde{q}$ is sufficiently close to q, then $N(\tilde{q}) = N(q)$.

(ii) If $q(x)$ is nondecreasing for $x > 0$, then $N(q) = 0$.

Such a stability as in (i) is fundamental in discussing perturbation of environments. Assertion (ii) implies that the bifurcation curve μ uniquely determines the reaction kinetics g in such a moderate environment q that an organism, e.g., a phytoplankton, suffers from an increasing amount of stress as it approaches the boundary of the habitat.

Now a question naturally arises: What kind of environment q yields a positive value of $N(q)$? A systematic method of constructing environments q with an arbitrary positive (even) degree of freedom N is developed in §5 of [6] by using some techniques from finite differences. Figures 4, 5 and 6 below visualize such constructions with $N = 2$ and 4, where $v_1(x)$ is the first eigenfunction, normalized so that $v_1(0) = 1$, of the linear Strum-Liouville equation (5) with the normalization of constants: $D = 1 = L$.

In §12 we will characterize the degree of freedom $N(q)$ as the cardinality of the zeros of a certain analytic function $\zeta_q(z)$ (see (10)).

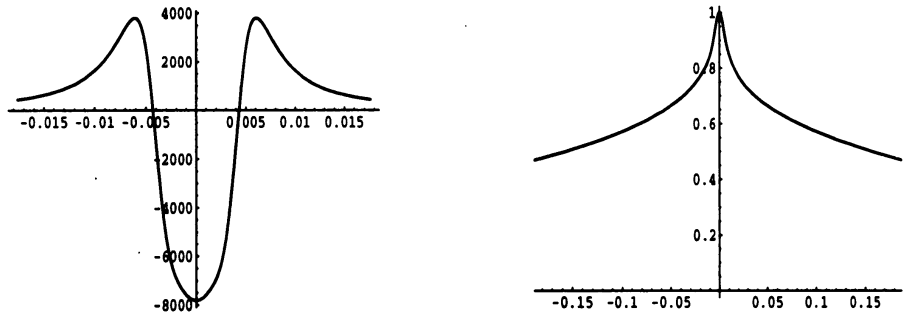

Figure 4: An environment $q(x)$ with $N = 2$ and its eigenfunction $v_1(x)$

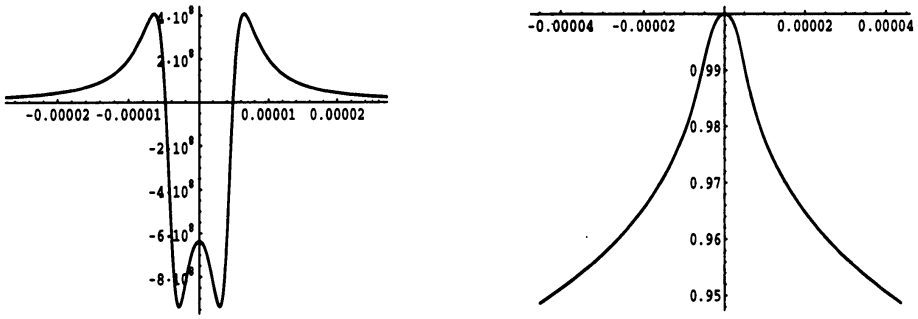

Figure 5: An environment $q(x)$ with $N = 4$ and its eigenfunction $v_1(x)$

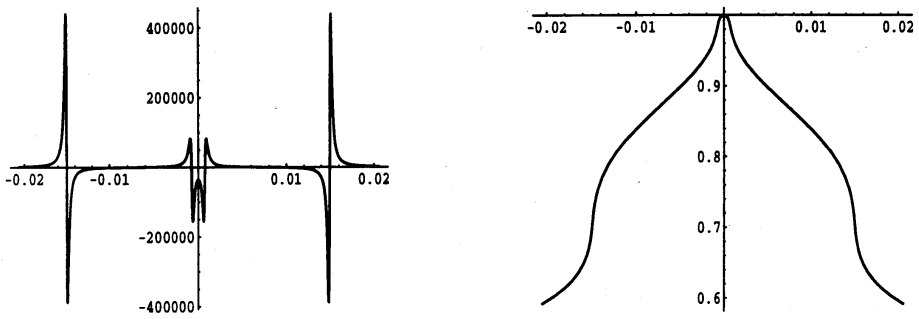

Figure 6: Another environment $q(x)$ with $N = 4$ and its eigenfunction $v_1(x)$

10 Biological Speculations

In general, an environment has an abundance of factors that depend on parameters describing, for example, physical, chemical, physiological, and/or social conditions. It is a challenging problem to single out a dominant factor controlling the degree of freedom $N = N(q)$ from so many factors of an environment q. An inspection of examples shows that an environment $q = q(x)$ has a tendency to *fluctuate* near the origin $x = 0$ more strongly as N is getting large. We are tempted to hazard a guess that a strong heterogeneity of an environment in a certain sense (which we have not yet been able to pinpoint) is a dominant factor that increases the magnitude of N. If so, a biological conclusion deduced from our analysis would be the robustness of an organism which adapts itself to a tough environment by arranging a flexibility in feasible kinetics.

11 Multiplicative Wiener-Hopf Equations

The mathematical analysis leading to our main results (Theorem 8.1) is based on a key observation that the linearized map $d\pi$ of the direct bifurcation map $\pi : g \mapsto \mu$ is essentially a kind of Wiener-Hopf integral operator.

Recall that a Wiener-Hopf operator K of usual type is expressed as

$$(Ku)(x) = \int_0^\infty k(x-y)\,u(y)\,dy \tag{7}$$

with some kernel $k(x)$. There is a large amount of studies on this type of operators (see Kreĭn [8, 9] and the references therein). Those operators were quite successfully applied to inverse scattering theory (see Marchenko [11]).

On the other hand, in investigating our inverse bifurcation problem, we encounter a Wiener-Hopf operator of *multiplicative* type, by which we mean an operator J_Φ of the form:

$$(J_\Phi u)(x) = \int_0^1 \Phi(t)\, u(xt)\, dt. \tag{8}$$

It is seen that (8) is reduced to (7) in the formal level by making a suitable transformation. In contrast to (8), we may say that (7) is of *additive* type.

In our inverse bifurcation problem, the kernel $\Phi(t)$ is given by

$$\Phi(t) = \frac{t}{v_1'(1)\, v_1'(v_1^{-1}(t))}. \tag{9}$$

It is expressed as $\Phi(t) = A\, t(1-t^2)^{-\frac{1}{2}} +$ (less singular terms), with some positive constant A. This exhibits that $\Phi(t)$ possesses a singularity at $t = 1$. We are thus motivated to develop a general theory for a class of singular multiplicative Wiener-Hopf operators. Whole the paper [5] and a good portion of [6] are devoted to such a general theory.

12 Main Ingredients of the Proof

We present the main ingredients of the proof of Theorem 8.1. They consist of an analysis of a multiplicative Wiener-Hopf operator and applications of implicit function theorems in an appropriate function spaces setting (as for the function spaces setting, we refer to §13).

(i) an analysis of the singular multiplicative Wiener-Hopf operator J_Φ with $\Phi(t)$ in (9) arising as the linearization of the direct bifurcation map:
- its Fredholm-ness;
- its surjectivity;
- dim (Ker J_Φ) = ♯ of the zeros of a certain analytic function $\zeta_q(z)$.

(ii) applications of implicit function theorems to the direct bifurcation map.

The function $\zeta_q(z)$ appearing in item (i) is defined by

$$\zeta_q(z) = \int_{-L}^{L} v_1(x;q)^z\, dx,$$

where $v_1(x;q)$ is the first eigenfunction, normalized so that $v_1(0;q) = 1$, of the linear Strum-Liouville equation (5). It is shown that $\zeta_q(z)$ is a holomorphic function with at most finitely many zeros in the right half-plane $\mathrm{Re}\, z > 0$.

The degree of freedom $N(q)$ is then characterized as the cardinality, counted with multiplicities, of the zeros of $\zeta_q(z)$ in the right half-plane $\mathrm{Re}\, z > 2 + \alpha$:

$$N(q) = \sharp\{ z \in \mathbb{C} : \zeta_q(z) = 0,\ \mathrm{Re}\, z > 2 + \alpha \}, \tag{10}$$

where $\alpha \in (0, 1/2)$ is the "Hölder index" of a relevant function space (see §13). Since $\zeta_q(z)$ is positive on the positive real axis, the zeros of $\zeta_q(z)$ appear in pairs of nonreal, mutually conjugate complex numbers. Hence, by (10), the degree of freedom $N(q)$ is a nonnegative even integer (see Figure 7).

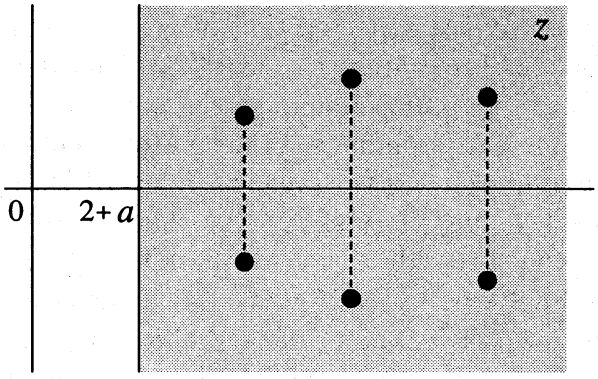

Figure 7: Zeros of $\zeta_q(x)$

13 Function Spaces Setting

Reaction kinetics g and bifurcation curves μ lie in *Hölder-like* function spaces. Given a number $\alpha \in (0, 1/2)$ and a finite interval $I = [0, b]$ with $b > 0$, let

$$\begin{aligned} X_\alpha &= \{ g \in C^1(I) : g(0) = g'(0) = 0,\ ||g||_{X_\alpha} < \infty \}, \\ Y_\alpha &= \{ \mu \in C(I) : \mu(0) = 0,\ \delta\mu \in C(I),\ ||\mu||_{Y_\alpha} < \infty \}, \end{aligned}$$

where $\delta = h\,(d/dh)$ is the Euler operator and

$$\begin{aligned} ||g||_{X_\alpha} &= \sup_{h \neq k} \frac{|g'(h) - g'(k)|}{|h - k|^\alpha}, \\ ||\mu||_{Y_\alpha} &= \sup_{h \neq k} \frac{|h^{3/2}\mu'(h) - k^{3/2}\mu'(k)|}{|h - k|^{\alpha + 1/2}}. \end{aligned}$$

Then X_α and Y_α become Banach spaces with norms $||\cdot||_{X_\alpha}$ and $||\cdot||_{Y_\alpha}$, respectively. Now our setting is that reaction kinetics g and bifurcation

curves μ belong to X_α and Y_α, respectively. The index $\alpha \in (0, 1/2)$ is chosen in such a manner that the function $\zeta_q(z)$ has no zeros on the vertical line $\mathrm{Re}\, z = 2 + \alpha$. We remark that this condition is satisfied except for at most finitely many numbers in the interval $0 < \alpha < 1/2$.

14 Perspective of Further Developments

We conclude this paper by discussing a few directions in which our work should be extended. First, the assumption of spatial symmetry in (3) does not seem to be essential; it is expected that our results remain valid without the assumption, but in this context the central density does not make sense and the *maximal density* should be employed instead.

Secondly, if the outer environment of the habitat is not completely hostile, then the Dirichlet condition in (4) should be replaced by a boundary condition of the third kind: $c_\pm v(\pm L) \pm v'(\pm L) = 0$, where $c_\pm$ are positive constants representing the rates of hostility. The authors have little knowledge as to whether our results will carry over in this case. If the environment is homogeneous, $q(x) \equiv 0$, and the boundary of the habitat acts as a perfect barrier (the Neumann condition: $c_\pm = 0$), then the inverse problem is immediately settled as $g(h) = h\mu(h)$, due to the fact that the reaction-diffusion equation cannot sustain a spatial pattern induced by the effect of diffusion (see §14.9 of Murray [13]). If the outer environment is somewhat hostile, $c_\pm > 0$, the integral equation we encounter is of an *incomplete* type and requires further analysis, although some parts of our arguments remain valid.

Finally, many realistic models of biological interest are multi-dimensional in space and multi-specific in populations. This fact makes the general inverse problem quite difficult, but ultimately such a general situation should come within the scope of our analysis.

References

[1] R.S. Cantrell and C. Cosner, *The effects of spatial heterogeneity in population dynamics*, J. Math. Biol. **29** (1991), 315–338.

[2] M.G. Crandall and P.H. Rabinowitz, *Bifurcation from simple eigenvalues*, J. Funct. Anal. **8** (1971), 321–340.

[3] M.G. Crandall and P.H. Rabinowitz, *Bifurcation, perturbation of simple eigenvalues and linearized stability*, Arch. Rat. Mech. Anal. **52** (1973), 161–180.

[4] K. Iwasaki and Y. Kamimura, *An inverse bifurcation problem and an integral equation of the Abel type*, Inverse Problems **13** (1997), 1015–1031.

[5] K. Iwasaki and Y. Kamimura, *Convolution calculus for a class of singular Volterra integral equations*, J. Integral Eqs. Appl. **11** (1999), 461–499.

[6] K. Iwasaki and Y. Kamimura, *Inverse bifurcation problem, singular Wiener-Hopf equation and mathematical models in ecology*, preprint (2001), 36 pages.

[7] H. Kierstead and L.B. Slobodkin, *The size of water masses containing plankton bloom*, J. Marine Research **12** (1953), 141–147.

[8] M.G. Kreĭn, *Integral equations on a half-line with kernel depending upon the difference of the arguments*, Amer. Math. Soc. Transl. (2) **22** (1960), 163–288.

[9] M.G. Kreĭn, *Topics in differential and integral equations and operator theory*, Operator Theory: Advances and Applications **7**, Birkhäuser-Verlag, Basel, 1983.

[10] D. Ludwig, D.G. Aronson, H.F. Weinberger, *Spatial patterning of the spruce budworm*, J. Math. Biol. **8** (1979), 217–258.

[11] V.A. Marchenko, *Sturm-Liouville operators and applications*, Operator Theory: Advances and Applications **22**, Birkhäuser-Verlag, Basel, 1986.

[12] G.M. Murray, Jr., *Population dynamics, Alternative models*, Academic Press, New York, 1979.

[13] J.D. Murray, *Mathematical biology*, 2nd. ed., Biomathematics **19**, Springer-Verlag, Berlin, 1993.

[14] A. Okubo, *Diffusion and ecological problems: mathematical models*, Biomathematics **10**, Springer-Verlag, Berlin, 1980.

[15] P.H. Rabinowitz, *Nonlinear Sturm-Liouville problem for second order ordinary differential equations*, Comm. Pure Appl. Math. **23** (1970), 939–961.

[16] L.B. Slobodkin, *A possible initial condition for red tides of the coast of Florida*, J. Marine Research **12** (1953), 148–154.

[17] J.G. Skellam, *Random dispersal in theoretical populations*, Biometrika **38** (1951), 196–218.